For What It's Worth: Reward Value Drives Visual Selective Attention

Failing, F.M.

2017

document version
Publisher's PDF, also known as Version of record

CHAPTER ONE

–

A Selective Review on the Influence of Reward on Attentional and Perceptual Processing

1.1. Introduction

Imagine you have recently made a new friend and want to visit her for the first time. Your friend, however, lives at the other side of the town so in order to visit her, you will have to drive through the busy city. While driving, looking for the road signs that tell you which way to go is a challenging task. You may have some idea as to what they look like or where to find them but, regardless, you will have to continuously search for them in a cluttered, crowded environment. To make matters worse, moving people or cars and flashy billboards or commercial signs will occasionally distract you from your task.

This everyday scenario illustrates the bottleneck in how and what information we can process. Many major theories assume that this bottleneck is resolved by attention (e.g. Carrasco, 2011; Theeuwes, 2010; Wolfe, 2007; Yantis, 2000). According to such theories, attention enables us to parse information that is critical in a given moment by prioritizing or suppressing stimuli selectively. Due to this property, selectivity of attention, as a construct comprising many different processes, molds subsequent mental as well as motor operations whether they are simple or complex.

In this thesis, I will present evidence which contributed to the emerging consensus that reward plays an active role in shaping attention. This evidence is derived from experiments in which we showed an influence of reward on attentional selection that cannot be explained in terms of otherwise known factors driving attentional selection (Chapter 2 through 4), is not restricted to spatial but extends to nonspatial attentional selection (Chapter 5), has similarities to how threat affects selection (Chapter 7) and, ultimately, affects how we perceive time (Chapter 6). In this introduction, I will review some of the critical concepts and studies relevant to these experiments and will embed their findings into the bigger picture of how reward contributes to our understanding of the world around us.

1.1.1. Top-down and bottom-up attentional control

Irrespective of whether we search the environment covertly (i.e. by shifting attention in space while our eyes remain stationary) or overtly (i.e. by moving our eyes), classic studies have isolated two categories of processes demarking how visual attentional selection is controlled. Thinking about the example of

how you search for road signs while driving to your friend, one intuitive way to categorize attentional control is in terms of one's own beliefs, goals or intentions. Indeed, it is obvious that attending certain cues (e.g. road signs) might help to achieve your goal of finding the way to your friend, while attending others (e.g. parked cars) may not. This so-called top-down (also called endogenous or goal-directed) attentional control is thought to be volitional and under the control of the observer at any given point in time (e.g. Posner, 1980; Treisman & Gelade, 1980; Theeuwes, 2010). Since these top-down processes are under volitional control, they usually take a considerable amount of time and effort.

Searching for road signs, however, is not a simple task when the streets are busy and time to search is limited. Flashy billboards next to the street or pedestrians suddenly crossing it might also attract your attention even though you were not actively searching for them. These are examples of bottom-up (also called exogenous or stimulus-driven) control in which selection is determined by the properties of the environment. In particular, physical salience of a stimulus relative to its immediate surroundings determines how likely it is that this stimulus "grabs", or captures, attention. The salience of a stimulus is usually defined in terms of low-level stimulus features such as luminance, orientation, color or motion (e.g. Treisman & Gelade, 1980, Itti & Koch, 2001). Contrary to top-down attentional control, bottom-up control is thought to occur involuntarily (i.e. independent of one's goals and intentions) but also far more quickly and effortlessly. Findings from studies on bottom-up attentional control are commonly interpreted in terms of a physically salient event or stimulus drawing attention on its own.

1.1.2. Priority maps: an integration of top-down and bottom-up processes

The dichotomy between top-down and bottom-up attentional control has sparked a great deal of research investigating its explanatory power by pitting the respective influence of both types of control against each other. For example, research demonstrated that when searching for a given target, physically salient distractors that are otherwise irrelevant for the task at hand can disrupt top-down control and capture attention (attentional capture, e.g. Theeuwes, 1992; Yantis & Jonides, 1990) as well as our eyes (oculomotor capture, e.g. Theeuwes, Kramer, Hahn & Irwin, 1998; Theeuwes, Kramer,

Hahn, Irwin, & Zelinsky, 1999; Yantis & Egeth, 1999). Such findings demonstrate that while we are often in control of how and what we search, bottom-up processes can affect our performance not only independently of top-down processes but even in spite of them (but see Bacon & Egeth, 1994; Folk, Remington & Johnson, 1992; Leber & Egeth, 2006; for the extant discussion on this matter).

Influential theoretical as well as computational models on attentional control assume a priority map in the brain (e.g. Bisley, 2011; Itti & Koch, 2001; Theeuwes, 2010; Wolfe, 2007; Zelinsky & Bisley, 2015). This priority map represents an integration of both, top-down and bottom-up, signals in a common priority space (for a schematic illustration see Figure 1). The highest peak of activation on the priority map corresponds to the spatial location which is most likely attended next. According to these models, attention is predominantly spatial (but see feature-based attention accounts, e.g. Maunsell & Treue, 2006; Theeuwes, 2013; Treue & Martinez-Trujillo, 1999) and hierarchical in the sense that the specific location with the highest activity on the priority map is most likely to attract attention first in a winner-takes-all fashion. Since physical stimulation may vary and top-down and bottom-up processes unfold differently over time, the priority map is subject to a constantly ongoing change in which peak activity on the map is shifting from one location to the next.

At the heart of the priority map concept lies the idea that its activity profile determines the outcome of the brain's intrinsically emergent property of competition for neural representation (Desimone, 1998; Duncan & Desimone, 1995). Selectivity of attention, according to the theory of biased competition, resolves the competition by biasing it in favor of the stimulus with the highest priority signal (e.g. Theeuwes, 2010). The notion that competition for neural representation is a dominant attribute along the entire hierarchy of the visual cortex might also explain why many different areas have been suggested to constitute a priority map (e.g. Balan & Gottlieb, 2006; Bisley & Goldberg, 2010; Li, 2002; Mazer & Gallant, 2003). It is, however, still a matter of debate to what extent the notion of a priority map corresponds to an actual map rather than to a metaphor summarizing and emphasizing key aspects arising from the attentional phenomenon (cf. Anderson, 2011; Duncan, 2006; Maunsell, 2015).

1.1.3. Selection history

Although the dichotomy of top-down and bottom-up attentional control accounts for a wide range of phenomena and has been a fundamental premise of influential theories, there is substantial evidence that some factors influence attentional selection in a way that does not fit this framework very well (Awh, Belopolsky, & Theeuwes, 2012). For instance, priming describes the effect by which a stimulus (feature) that has been repeatedly attended in the recent past is more efficiently selected and identified on the current trial (Maljkovic & Nakayama, 1994; Tulving & Schacter, 1990). Priming is well-documented in terms of its low-level facilitatory effect on perceptual processing. Maljkovich and Nakayama (1994), for example, demonstrated the influence of priming in the context of a search task (see also Hillstrom, 2000; Olivers & Humphreys, 2003). Priming between trials, or intertrial priming, occurred for up to eight successive trials, even when participants were unware of repetitions (Maljkovich & Nakayama, 2000), or even when they were informed that the target was unlikely to be same between trials (Maljkovich & Nakayama, 1994).

Another powerful demonstration of how previous affects current selection comes from Chun and Jiang (1998) who showed the importance of the context in which the selected stimulus is embedded. They demonstrated that when targets appeared in contextual configurations in which they had been selected before, they were selected more quickly than when they appeared in configurations in which they had never been selected – even though participants were completely unaware of the contextual relationships. There is now ample evidence suggesting that contextual cueing, much like intertrial priming, occurs independent of the currently active task-set, task-relevance or salience of a stimulus (Chun, 2000).

Findings such as intertrial priming (Kristjansson & Campana, 2010) and contextual cueing (Chun, 2000) do not fit the traditional dichotomy very well since their influence can be observed even if top-down and bottom-up processes are controlled. However, these findings can be understood when embracing the idea that some form of a memory process can shape current selection on its own (i.e. independent of known top-down and bottom-up factors). This notion led to the proposal of a third category of factors contributing to the activity on the priority map (see Figure 1; Awh et al., 2012; cf. Chun, Golomb, & Turk-Browne, 2011). According to this proposal,

attentional selection is jointly determined by top-down, bottom-up and selection history processes.

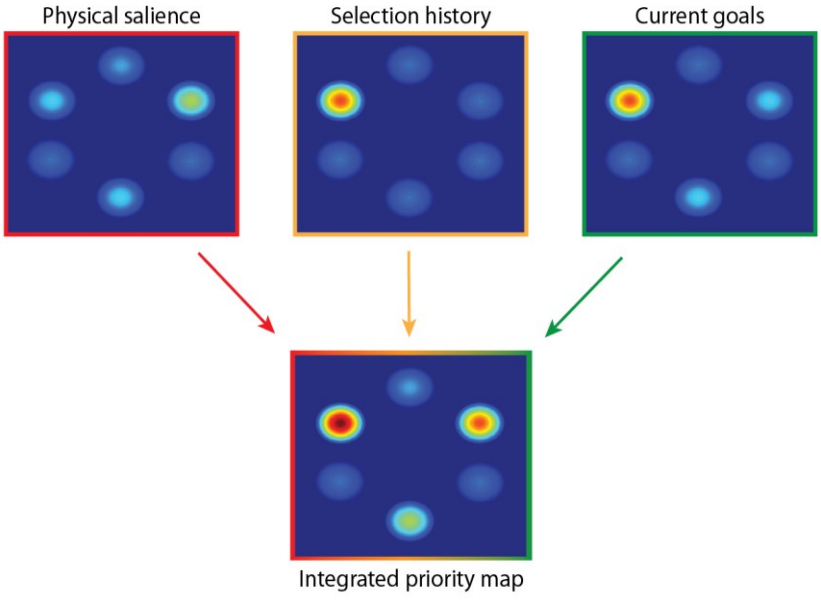

Figure 1. Schematic illustration of an integrated priority map. The priority signal of each stimulus location is computed according to its underlying type of process (i.e. top-down, bottom-up or selection history) and eventually integrated in a priority map that determines selection. The stimulus location with the strongest signal on this priority map will be attended (here the top-left corner). Each type of input is presumed to contribute independently to the priority map allowing combined but also diametrically opposed effects. In this example, higher priority is represented by "warmer" colors. Adapted from Awh et al., (2012).

1.2. Attention and reward

As early as 1911, Thorndike postulated the 'law of effect' (Thorndike, 1911, p. 244), which stated that behavioral responses soliciting a reward will become strengthened or habitual (cf. instrumental or operant conditioning). Not long after Thorndike, Pavlov (1927) observed that stimuli reliably predicting reward would eventually start to elicit a behavioral orienting response (cf. Pavlovian or classical conditioning). While, at the time, overt behavior and the processes of learning were the focus of research, later, other researchers started trying to understand what internal states accompanied the strengthening of response patterns due to reward (e.g. Simon, 1967). This led to theories on how rewards motivate behavior as well as internal states (e.g. Berridge & Robinson, 1998; Mackintosh, 1975; Pearce & Hall, 1980). What

has become increasingly evident in recent studies on attention is that similar principles as those formulated in the classic theories may hold for how reward influences attention.

1.2.1. Reward as a motivational incentive

In the animal world, survival depends on how effective animals are in obtaining rewards such as water, food or sex. Typically, when reward is expected, for instance as an incentive for performing a specific task, animals (including humans) perform better than when no reward is expected (Wise, 2004). A beneficial influence of incentive reward is observed in a variety of tasks and has been shown to impact behavior in different ways irrespective of whether it is considered a primary (e.g. food or water) or secondary reinforcer (e.g. money or social approval).

Traditionally, incentive rewards have been studied in the context of cognitive control which refers to the set of functions that encode and maintain the representation of the current task set (i.e. currently relevant stimulus-response and action-outcome associations or goals; Botvinick & Braver, 2015). This set of functions is comprised of a variety of components involving memory, action and attention. The influence of incentive reward on either of these components has been a topic of extensive research which revealed a strong connection between incentive reward and cognitive control. For instance, incentives have been shown to improve response preparation and inhibition (e.g. Boehler, Schevernels, Hopf, Stoppel, & Krebs, 2014; Mir et al., 2011), enhance the control of episodic memory encoding and retrieval (e.g. Patai, Doallo, & Nobre, 2012) and increase adaptation to errors or other cognitive conflict (e.g. Stürmer et al., 2011; Braem, Verguts, Roggeman, & Notebaert, 2010; for a more detailed review see Botvinick & Braver, 2015). More important for the scope of this introduction is, however, that incentive rewards have also been demonstrated to strongly influence attentional control. For instance, Engelmann and Pessoa (2007) showed in a spatial cueing task (Posner et al., 1980), that participants had a higher detection sensitivity in blocks in which they were informed that good performance was rewarded compared to blocks in which they knew it was not (see also Engelmann, Damaraju, Padmala, & Pessoa, 2009; Milstein & Dorris, 2007; Small et al., 2005). Padmala and Pessoa (2010) demonstrated in a Stroop-task that, when reward was at stake, target selection was facilitated on distractor congruent

trials and interference in target selection was smaller on distractor incongruent trials. Studies like these suggest that incentives improve performance via motivating strategic processes such as the preparation of an appropriate attentional or oculomotor orienting response (e.g. Engelmann & Pessoa, 2007; Milstein & Dorris, 2007; Sawaki, Luck, & Raymond, 2015; Small et al., 2005) or facilitating selective attenuation of irrelevant attentional distractors (i.e. attentional filtering; Padmala & Pessoa, 2008; 2010).

Neuroimaging studies have linked incentive-induced changes in neuronal activity to brain regions and electrophysiological markers that are usually observed when manipulating traditional factors of attentional control. For example, an fMRI study by Small et al. (2005), which used a spatial cueing task, observed widespread activations of task-specific regions in response to reward-signaling cues presented prior to a given trial. As would be expected from a cueing task, many brain areas considered to be important in the orienting of visuospatial attention showed increased activity when reward was at stake. The implication, then, is that strategic and task-specific processes (i.e. the orienting of spatial attention) were more vigorously prepared throughout the interval between cue and search display onset and, as a consequence, task performance improved. Corroborating electrophysiological evidence comes from a study by Sawaki and colleagues (Sawaki, Raymond, & Luck, 2015). They observed reduced alpha power for high relative to low reward trials during a preparatory interval (i.e. an interval after the offset of reward incentive cues and before the onset of the search display). The authors argued that this reflected visual alertness, or increased cognitive effort to focus attention, for the upcoming search task. Indeed, subsequent to the onset of the search display, the target-elicited N2pc component, thought to reflect attentional selection and originating in extrastriate visual areas such as V4 (e.g. Eimer, 1996), was smaller on high than on low incentive trials. This is consistent with the typical finding of a generally reduced N2pc in easy versus hard search tasks (Eimer, 1996; Luck & Hillyard, 1994) and led Sawaki and colleagues to argue that the preparation interval allowed for more efficient attentional processing when more reward was at stake which then reduced the need for focused attention.

In another type of studies incentive reward has been shown to impact attention more selectively. In contrast to the previous studies, in which attentional control is more broadly affected, these studies showed modulations in attentional selection for the specific perceptual features or spatial location

of targets that were associated with reward. In such studies, participants typically receive reward if they successfully attended a specific stimulus (feature) or its location in order to perform a given task, thereby forming an association between a stimulus (feature) and reward (e.g. Kiss, Driver, & Eimer, 2009; Krebs, Boehler, & Woldorff, 2010; Kristjansson, Sigurjonsdottir, & Driver, 2010; Serences, 2008). Here too, response times are typically quicker and performance is more accurate when either a feature of a valid cue or the target itself is associated with a larger reward. For instance, in Kiss and colleagues (2009) participants had to search for a color singleton diamond (e.g. green) among diamonds that all had the same but a different color (e.g. red) and identify whether a small notch was on the top or the bottom of the target. Critically, participants were rewarded for correct and quick target identification but the magnitude of reward depended on the color of the target. One particular color (e.g. red) was associated with high reward and another (e.g. green) with low reward. Clearly distinct to other incentive reward studies was that not only the appropriate response but also the (magnitude of the) reward itself was uncertain up until the presentation of the target (i.e. trials with different outcomes were interleaved rather than blocked). Nevertheless, the results showed faster identification for high reward targets than for low reward targets. Importantly, electrophysiological recordings showed that the N2pc component was also modulated by reward magnitude. The N2pc was earlier and larger in response to high reward targets compared to low reward targets. These findings support not only the notion of preferential processing but also of a prioritized attentional state for reward-signaling targets when selection among multiple competing stimuli is necessary. By demonstrating this degree of selectivity on such a short time scale, these studies rendered alternative explanations of incentive reward effects solely in terms of global arousal unlikely.

Irrespective of whether reward was signaled prior to a block of trials, prior to an individual trial or contingent on the target, the beneficial effects found in all these studies can be readily explained in terms of ongoing top-down attentional control processes (e.g. Maunsell, 2004; Stanisor, van der Togt, Pennartz & Roelfsema, 2013). In one type of studies, time intervals allowed for alertness or strategic preparation of efficient attentional control. In other studies, participants actively and strategically searched for the stimulus signaling reward because it was the target or in any other way relevant for task performance (e.g. because it was bound to the spatial location of the target). Additionally, the reward-associated stimulus (feature) was also

the motivated target as it is the intrinsically motivated – in some studies even instructed – goal to obtain as much reward as possible.

Conjointly these studies therefore provide evidence for incentive-induced modulation of the top-down task-set. The prospect of reward can either broadly strengthen the task-set when reward is generally at stake, or more selectively affect components of the task-set, such as the representation of the target template or appropriate response, when reward is associated with specific feature or the location of the target. Concurring evidence for this notion comes from recent neuroimaging studies that demonstrated more accurate decoding of task-set representations in frontoparietal regions on reward incentive trials than on trials in which no reward could be earned (Etzel et al., 2015; Wisniewski et al., 2015). Critically, improvements in behavioral performance due to differential reward were shown to be statistically mediated by better task decoding (i.e. MVPA classification accuracy). In other words, stronger task-set representations due to incentive reward predicted better task performance.

In conclusion, studies have provided overwhelming evidence for a widespread influence of incentive reward on executive functioning and, more broadly, cognitive control which is also observed on the level of attentional control (Botvinick & Braver, 2015). The prospect of earning reward leads to strategic changes in top-down attentional control which subsequently have a beneficial effect on perceptual as well as attentional processing. This notion is in line with findings showing that incentives ultimately benefit attentional processing (e.g. Kiss et al., 2009) as well as enhance the perceptual representation of reward-associated targets (e.g. Serences, 2008). Recent evidence shows that these changes in processing are mediated by an enhancement of endogenous task-set representation in frontoparietal regions (Etzel et al., 2015; Wisniewski et al., 2015) which promotes task performance either more broadly or selectively depending on the specific task-demands.

1.2.2. Reward counter-acting top-down processes

In the studies discussed in the previous section, rewards were always congruent (i.e. not detrimental) to task demands. Observing performance benefits when either reward was generally at stake (i.e. in a reward block) or directly tied to the target or otherwise task-relevant stimulus might therefore

not come as a surprise: it makes strategically sense to selectively prioritize the reward signal for attentional selection in order to ensure a higher rate of success with the added benefit of earning larger reward. But how is performance affected when reward is not tied to a task-relevant stimulus or when attending a reward-signaling stimulus is counterproductive for obtaining reward? In other words, does the reward signal compete with other attentional control processes for attentional selection or is it merely modulating the efficacy of top-down control?

In this section I will discuss recent studies pitting reward against known top-down or bottom-up processes. I will first start by reviewing evidence from three different type of studies that were designed to disentangle reward from top-down control, before converging their findings onto a common functional mechanism. These studies provide evidence which suggests that reward shapes covert as well as overt attention independently of top-down and bottom-up processes.

1.2.2.1. Intertrial reward priming

An association between a stimulus and a reward implies the involvement of some sort of a memory process and the idea that such a process is capable of shaping attentional selection is not new. As mentioned before, selection history, for instance in the form of (intertrial) priming, is a powerful way by which current selection can be biased toward stimuli that have been selected in the past irrespective of other concurrently active attentional control processes. Only recently, however, perceptual priming has been shown to be further modulated by reward outcomes. For instance, experiments by Della Libera and Chelazzi (2006) demonstrated modulations of global and local stimulus priming by reward, such that stimuli, for whose inhibition participants were rewarded, were subsequently harder to select (cf. Della Libera & Chelazzi, 2009).

Even more convincing evidence of reward's influence on priming was provided by Hickey and colleagues (Hickey, Chelazzi & Theeuwes, 2010). This study was based on the additional singleton paradigm of Theeuwes (1991, 1992): a speeded task in which participants have to identify the orientation of a line segment placed inside a shape singleton object (e.g. a diamond among circles). The distractor, or additional singleton,

in this task, is defined by its physically salient color (e.g. a red shape among green shapes) – a feature that is task-irrelevant on every trial. The traditional finding of this task is that the distractor captures attention in a bottom-up fashion (i.e. causes interference in search time for the target) because it is physically the most salient item in the display (Theeuwes, 1991; 1992). Since target- and distractor-associated features can swap between trials, another classic finding of the additional singleton paradigm is intertrial priming. If target- and distractor-associated features swap from one trial to another, capture by the distractor is larger since its feature was recently associated with the target (e.g. Pinto, Olivers, & Theeuwes, 2005). Crucially, however, using this paradigm Hickey and colleagues showed that reward mediates the intertrial priming effect. When participants received a high reward, they were quicker in searching the target on the subsequent trial if no swap between the color associated with the target and the distractor occurred, but slower if a swap occurred. Conversely, when participants received a low reward, they were slower in searching the target on the subsequent trial if no swap occurred, but quicker if a swap occurred. Hickey and colleagues explained this finding in terms of relative revaluation and devaluation of perceptual features characterizing the target due to short-term reward history.

Remarkable about intertrial reward priming is its seemingly automatic nature. This notion was particularly evident in a follow-up experiment (Hickey et al., 2010) in which participants engaged in the same task but, this time, were explicitly told that whenever a high reward was earned, the colors associated with the target and the distractor would swap. There was, therefore, absolutely no incentive to strategically search for the feature recently associated with reward as it would provide only redundant (i.e. already known) information. As a matter of fact, attending it would hamper target search and reward payout since it would be more difficult to identify the target in time. In spite of that, reward-mediated intertrial priming occurred: participants could not help but preferentially attend the object of the same color as the high reward target on the previous trial even if it was no longer the target.

Strong neuronal evidence that recent reward history changes the perceptual and attentional processing of the reward-associated feature were provided from electrophysiological recordings in the same study (Hickey et al., 2010). Not only was there an enhanced P1 component, which is thought

to reflect increased early visual processing in extrastriate cortex without attentional modulation (cf. Hillyard, Vogel, & Luck, 1998; Luck & Hillyard, 1994b), but also a larger N2pc in response to the stimulus recently associated with high reward. This suggests that, by mediating perceptual priming, reward affects the representation of a stimulus rendering it more salient within the visual system.

Intertrial reward priming has since then been demonstrated to affect covert search even under more realistic circumstances such as when searching an object (e.g. a car) in a natural scene (e.g. a busy city street; Hickey, Kaiser, & Peelen, 2015). Overt search has also been shown to be affected by intertrial reward priming as evidenced by modulations in oculomotor capture as well as saccadic trajectories due to reward (Hickey & van Zoest, 2012; 2013). These reports underscore the large degree of generalizability and universality of intertrial reward priming and its immediate effect on attentional selection.

In summary, studies on intertrial reward priming provide evidence that reward mediates perceptual priming independently of active top-down processes. They furthermore support the idea that reward-based selection history impacts stimulus representation: reward changes the stimulus' pertinence to the visual system, prioritizing its perceptual and attentional processing irrespective of whether this serves top-down control or the acquisition of reward.

1.2.2.2. Value-driven attentional capture

Intertrial reward priming studies provide some evidence that rewarding attentional selection of a specific stimulus (feature) creates reward-based selection history which influences future selection. Albeit short-lasting (i.e. only evident on the following trial), this cannot be readily understood in terms of on-line active top-down processes. However, one may argue that because participants received reward throughout the entire experiment and were every so often rewarded for the selection of the feature that would shortly thereafter function as distractor, intertrial reward priming studies merely demonstrate limitations in flexibly adjusting top-down control. Similarly, the stimuli imbued with short-term reward-based selection history were often physically salient, mandating their attentional selection independently of reward-based selection history.

In another line of research, studies aimed to address these and other drawbacks of investigating the influence of reward on attentional selection in the context of intertrial priming. These studies focused on investigating how long-lasting the influence of reward-based selection history is and whether it would even be evident if reward is no longer available. In a now seminal series of studies by Anderson and colleagues (Anderson, Laurent, & Yantis, 2011a; 2011b), experiments were always split up into two different sessions (cf. Della Libera & Chelazzi, 2009). In the first, the so-called training session, participants had to search for a red or a green circle presented among differently colored non-target circles and report the orientation of a line segment inside that circle. During this session, the target of one color (e.g. red) was probabilistically (80% of the trials) rewarded with a high monetary reward and the target of another color (e.g. green) was probabilistically (80% of the trials) rewarded with a low monetary reward. In the subsequent test session, participants had to search for a shape singleton presented among randomly colored non-target shapes (a variant of the additional singleton task; e.g. Theeuwes, 1992). Critically, on two-thirds of the trials, one of the non-targets was rendered in either one of the colors of the target during the training session (i.e. red or green). The results showed that, during the test session, there was an increase in time to find the target when a non-target had a color that was previously associated with a high reward relative to when none of the previously reward-associated colors was present. There was, however, no significant difference when comparing trials on which there was a high reward distractor with trials on which there was a low reward distractor. This effect occurred even though participants were explicitly instructed to ignore any color information and were informed that they could no longer receive reward during the test session. Importantly, search time increased although the stimuli previously associated with reward were physically not more salient than any of the other non-targets. Indeed, the target was always the most physically salient item in the display. Anderson and colleagues argued that the increase in search time was due to attentional capture by the stimulus previously associated with high reward which could neither be explained in terms of top-down nor in terms of bottom-up processes (e.g. Anderson et al., 2011a). Although initially only demonstrated when both sessions occurred on the same day, subsequent studies showed that such interference can be observed up to six months after the training session (e.g. Anderson & Yantis, 2013).

Failing and Theeuwes (2014; see also Chapter 2 of this thesis) expanded the evidence for involuntary attentional orienting toward previously

reward-associated stimuli by demonstrating performance costs and benefits in the context of a spatial cueing experiment. Finding such costs and benefits is considered direct evidence for shifts of spatial attention (e.g. Posner & Cohen, 1984; Posner, Snyder, & Davidson, 1980) precluding alternative explanations of interference in search performance due to, for instance, non-spatial filtering costs (cf. Kahneman, Treisman, & Burkell, 1983). Their findings moreover demonstrated that capture is truly the result of reward-based selection history rather than selection history per se – an important refinement of Anderson and colleagues' findings (also Rutherford, O'Brien, & Raymond, 2010). Indeed, Anderson and colleagues failed to find a significant difference between high and low reward trials and only observed capture when comparing them to trials in which none of the stimuli that was consistently selected and rewarded throughout the training session, was present. The design by Failing and Theeuwes, however, allowed for comparing conditions in which stimuli were equally often selected during the training session (i.e. the stimuli had identical selection history) but only differed in the reward magnitude previously tied to their selection. The results showed that stimuli for whose selection participants were rewarded throughout the training session indeed captured attention in spite of concurrently presented stimuli that were equally often selected but not rewarded during the training session. Consistent with the assumption that it was the reward learning during the training session that caused capture during the test session, participants who showed a larger reward effect during learning (i.e. facilitated selection of the reward-associated target) also showed a larger reward effect during the test session (i.e. more capture by the reward-associated cue). Concurring findings by a recent study showed that, even if tasks in both sessions are unrelated, individual differences in the learning rate about a reward-associated stimulus feature during the training session are associated with the extent to which the stimulus causes capture during the test session (Jahfari & Theeuwes, 2016). This study found that participants who updated their beliefs more robustly after high rewards (i.e. showed steeper learning rates in the context of a hierarchical Bayesian reinforcement model) during reward learning, showed larger capture by the previously high rewarded stimulus during the test session.

Reward-based selection history created during a separate training session has also been demonstrated to influence overt search. Target objects associated with relatively high reward during a training session cause more oculomotor capture compared to objects previously associated with low

reward when presented as a task-irrelevant distractor in a subsequent test session. Oculomotor capture due to reward-based selection history has been observed when participants are unconstrained where to look at (Anderson & Yantis, 2012; Bucker, Silvis, Donk, & Theeuwes, 2015) or when instructed to search for a target defined by a different feature (e.g. color) than the one previously associated with reward (e.g. orientation; Theeuwes & Belopolsky, 2012).

Electrophysiological studies support the notion that stimuli imbued with reward-based selection history have preferential status in perceptual and attentional processing. For instance, Qi and colleagues (Qi, Zeng, Ding & Li, 2013) showed that the N2pc component was larger in response to distractors previously associated with a high reward. Interestingly, they found no modulation of the N2pc on fast trials but, instead, a larger Pd component, which is thought to index attentional suppression (e.g. Sawaki, Geng, & Luck, 2012). The authors argued that only if successfully suppressed, selection of the stimulus previously associated with high reward could be prevented. Converging evidence for a change in how previously reward-associated stimuli are processed comes from another study demonstrating modulations in the P1 component due to reward-based selection history up to seven days after the initial training session (MacLean & Giesbrecht, 2015). In line with the idea of increased perceptual processing, previously reward-associated stimuli elicited a larger P1. Interestingly, modulations in the P1 were moderated by task-relevance suggesting that at least parts of the early perceptual effect of reward-based selection history may underlie interactions with top-down processes.

A recent study using separate training and test sessions provides evidence that changes in perceptual and attentional processing of previously reward-associated stimuli can be localized in areas critically involved in representing selection priority. Anderson and colleagues (Anderson, Laurent, & Yantis, 2014) showed that previously reward-associated stimuli evoke activity in extrastriate cortex as well as the intraparietal sulcus, both critical to attentional control (e.g. Serences et al., 2005). Since the intraparietal sulcus (IPS) has been suggested to map priority signals for attentional selection, this indicates that the reward-based selection history signal persists to be neuronally represented even if reward is no longer available.

In conjunction, all these experiments make a strong case for what has since been referred to as value-driven attentional capture (VDAC; Anderson, 2013). A great wealth of studies has continued to explore the specificity and extent of this long-lasting reward effect demonstrating its influence on a variety of low-level features as well as on more complex stimuli such as faces, objects or visual scenes (for excellent reviews see e.g. Anderson, 2013; 2016; Chelazzi, Perlato, Santandrea, Della Libera, 2013). An important difference to the studies on intertrial reward priming is that the stimuli no longer signaled any reward but still – even after months – were prioritized for attentional selection. Moreover, the stimuli previously associated with reward were task-irrelevant and physically non-salient throughout the designated test session. The fact that there was, according to classic theories on attentional control, absolutely no reason to attend these stimuli, neither in the sense of top-down or bottom-up attentional control nor in terms of maximizing reward outcomes, provides strong evidence for a separate class of priority signal in attentional selection (Awh et al., 2012). This priority signal is shaped by reward-based selection history and has a long-term impact on perceptual as well as attentional processing.

1.2.2.3. Value-modulated attentional capture

A critical factor in the experimental design of the VDAC studies is that the stimulus associated with reward has instrumental value during the training session. In other words, similar to the design of incentive reward studies, reward is obtained when successfully selecting the reward-associated target throughout the training session. Prioritized selection of the previously reward-associated stimulus as observed during the subsequent test session can therefore be understood in terms of an instrumentally conditioned response (cf. Thorndike, 1911) or habitual orienting response instigated by reward ("attentional habit", see Anderson, 2016; Le Pelley, Mitchell, Beesley, George, & Wills, 2016) which is carried over from the training session. In other words, since selection of the reward-associated stimulus is task-relevant during the training session, capture in the test session may merely be the result of a lingering tendency to prioritize the previously task-relevant stimulus.

Recent scientific efforts focused on investigating whether VDAC is simply the result of an instrumental relationship or, alternatively, may also be due to a Pavlovian relationship between stimulus and reward. For instance, a

primate study addressed this question by rendering the reward signal orthogonal to any top-down factor (Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009). In other words, a reward-signaling cue, which preceded the onset of the target, could coincide with but was not predictive of the location of the target stimulus whose successful selection garnered the signaled reward. Indeed, this study showed that these reward-signaling cues with no instrumental value biased oculomotor selection in monkeys. In line with the idea that the association of reward changes the stimulus representation in the visual system, neurons in the lateral intraparietal cortex (LIP; i.e. the monkey analog of the human IPS) exhibited preferential firing for cues which consistently predicted reward. However, while the reward signal may have been orthogonal to the location of the target, strategically prioritizing selection of reward-associated stimuli was also not tied to any costs for task performance or reward payout; especially because the reward-signaling cue preceded the target onset and thus did not immediately compete with the target. Under such circumstances, it is known that primates strategically search for the reward-associated cue (Bromberg-Martin & Hikosaka, 2009).

A recent series of studies by Le Pelley and colleagues, however, investigated whether a reward-signaling stimulus competes for attentional selection even if it never coincided with the target location on a given trial and even if its selection never resulted in reward (Le Pelley, Pearson, Griffiths, & Beesley, 2015; Pearson, Donkin, Tran, Most & Le Pelley, 2015; for a conceptually similar approach in the context of a training and test session design see Mine & Saiki, 2015, Experiment 2). Therefore, there was not only never a benefit from selecting the reward-signaling stimulus under these circumstances but actual costs equivalent to deteriorated task performance and less reward payout. The experimental paradigm used in these studies was based on the additional singleton task (Theeuwes, 1992): participants were required to search for a shape singleton while a color singleton, varying in color (e.g. blue or red) and present on two-thirds of the trials, had to be ignored. The critical manipulation was that the color of the color singleton distractor signaled the magnitude of the reward which could be earned if participants would give the correct response within a given time limit. As there was no separate training session, the stimulus signaling reward was task-irrelevant throughout the entire experiment and was also never required to be attentionally selected in order to obtain reward. Le Pelley and colleagues reasoned that if any capture by that stimulus was to be found, it must have been due to a Pavlovian association between the distractor and the reward it

signaled (Le Pelley et al., 2015; Pearson et al., 2015). Indeed, the results showed that attentional capture, measured as the interference in RT when comparing distractor versus no distractor trials, was larger when the distractor signaled a high compared to a low reward. In a follow-up eye movement study in which reward was omitted if participants would look at the reward-signaling color singleton, similar results were obtained. Here too, color singleton objects which were task-irrelevant throughout the entire experiment caused more often a reward omission when they signaled high relative to low reward.

Even though the results were compelling, one specific design feature of the studies by Le Pelley and colleagues makes it difficult to conclude involuntary capture due to Pavlovian reward associations. Since the reward-signaling distractor in their studies was always physically the most salient object in the display, it is expected that the saliency of the distractor itself drove initial selection (e.g. Theeuwes, 1992). As noted earlier, it is well-documented that physically salient stimuli "pop out", capturing attention both covertly and overtly in a reflexive manner (Theeuwes, 2010). Consequently, this raises the possibility that if the stimulus signaling reward would not have been physically salient, Le Pelley and colleagues would not have observed any attentional capture by the reward-signaling stimulus. Failing and colleagues (Failing, Nissens, Pearson, Le Pelley, & Theeuwes, 2015; Failing & Theeuwes, submitted; see Chapter 3 and 4; see also Bucker, Belopolsky, & Theeuwes, 2015) addressed this issue by demonstrating that even if the task-irrelevant but reward-signaling stimulus is physically non-salient throughout the entire experiment, one does observe attentional (Failing & Theeuwes, submitted) as well as oculomotor capture (Failing et al., 2015) by that stimulus. Critically and further supporting the notion of an involuntary bias toward reward-signaling stimuli, particularly the early first saccades have been shown to be prone to capture by high relative to low reward distractors (Failing et al., 2015).

Importantly, Failing and Theeuwes (submitted, see Chapter 4) only observed attentional capture if participants were either informed about the task-irrelevant and physically non-salient feature that signaled reward or if participants became aware of the association during the experiment. On a broader scale, this suggests that in order to trigger learning about the reward-signaling stimuli, these stimuli first have to be prioritized for attentional selection. Failing and Theeuwes suggested that the initial prioritization needed

to trigger learning was achieved differently in different type of studies. Some studies rendered the reward-signaling stimulus task-relevant throughout a training session (cf. VDAC studies; e.g. Anderson et al., 2011b), others rendered it physically salient (e.g. Anderson et al., 2011a; Hickey et al., 2010; Le Pelley et al., 2015) and again others relied on awareness of the stimulus-reward association (Failing & Theeuwes, submitted). It is important to note that this attentional prioritization is merely needed to trigger learning. Once the association between stimulus and reward is established, involuntary capture due to reward occurs independently. In other words, after initial prioritization by either top-down task-relevance, bottom-up physical salience or awareness of the stimulus-reward association and sufficient learning, the reward association alone is sufficient to bias attention independent of other top-down or bottom-up factors. Conjointly, this notion strongly supports the idea that learning must first occur and that this learning process induces a long-lasting change in the representation of the reward-associated stimulus such that it becomes more salient which in turn prioritizes the stimulus for attentional or oculomotor selection.

In short, the above presented studies provide conclusive evidence for a different form of reward-driven attentional capture which has since then been referred to as value-modulated attentional capture (Le Pelley et al., 2015; Pearson et al., 2015; Pearson et al., 2016). They demonstrate conclusive evidence that Pavlovian associations can govern attentional selection priority due to reward. Research has just started to investigate if and how this form of reward priority signal comes about. Further research will have to focus on the underlying neuronal processes that accompany this form of priority signal in order to map out putative differences to how reward priority is created through intertrial reward priming or instrumental conditioning.

1.2.2.4. An overarching mechanism: reward changes stimulus representations

Reward is critically involved in cognitive control and yet we have seen that there is mounting evidence for an influence extending beyond the instigation of strategic attentional control. Reward affects attentional selection in a way that cannot be explained in terms of active top-down control as stimuli associated with reward have been shown to disrupt performance even when known strategies to avoid interference were available and better for obtaining

reward. Plenty of studies have now demonstrated that this influence can also not be explained in terms of bottom-up processes: reward affects attentional selection in spite of top-down factors even if physical salience is controlled. Therefore, attention is involuntarily drawn towards stimuli that either currently or have previously signaled reward independent of concurrently active top-down or bottom-up processes.

These findings give rise to the idea that reward changes the representation of a stimulus through (repetitive) association. This association can be established via instrumental or Pavlovian learning and impinges upon stimulus representations on the level of simple features as well as more complex set of perceptual features, such as in objects or scenes. The change in stimulus representation is reminiscent of a facilitatory priming mechanism driven by reward which renders a reward-associated stimulus more salient to the visual system.

The notion of a change in the stimulus representation due to reward is akin to how Berridge and Robinson proposed "incentive salience" to come about (Berridge & Robinson, 1998; Berridge, 2007). According to the incentive salience hypothesis, a theory grounded in research on addiction, incentive salience is "wanting": a property in the brain associated with a stimulus that reliably predicts reward. Incentive salience transforms an otherwise neutral or intrinsically insignificant stimulus into a stimulus that grabs attention because it signals a wanted outcome (cf. Berridge & Robinson, 1998; for a similar theory grounded in the field of associative learning see "the predictiveness principle" in Le Pelley et al, 2016, or Mackintosh, 1975).

Neuroimaging studies have indeed provided substantial evidence for a change in the neuronal representation of a reward-associated stimulus. These changes are reflected in modulations in neuronal firing such that neuronal activity in response to stimuli imbued with incentive salience is elevated along the visual hierarchy as early as (extra)striate cortex (e.g. Anderson et al., 2014; Hickey et al., 2010; Seitz & Watanabe, 2009; Serences, 2008; Serences & Saproo, 2010; Qi et al., 2013). For example, a recent study demonstrated modulations in the pattern activity of a reward-associated stimulus that was specific to the pattern evoked by the stimulus before it was associated with reward. Using fMRI and MVPA in the context of a naturalistic search task, Hickey and Peelen (2015) showed that information about distractor objects associated with reward was suppressed in the object-selective cortex (OSC;

i.e. lateral-occipital complex). In line with this finding, there were larger performance costs due to the reward-associated distractor in participants who showed less suppression of that distractor object in OSC. This supports the idea that a stimulus associated with reward gains incentive salience, changing its neuronal representation such that the suppression of its representation is necessary to prevent it from capturing attention. This idea also dovetails with earlier findings on intertrial reward priming in which greater activation of a reward-associated stimulus, indexed by a larger N2pc, was quickly followed by a suppression in the visual response to it (Hickey et al., 2010; for similar findings in the context of VDAC see, e.g. Qi et al., 2013).

In terms of attentional control, the concept of a changed stimulus representation (or gained incentive salience) connects well with the idea of (reward-based) selection history (Awh et al., 2012). Through repeated reward-driven attentional selection, a stimulus gains priority in subsequent selection making it easier and faster to search for it when it is the search target. Conversely, though, such a stimulus also becomes much harder to ignore when it is a distractor presented simultaneously with the target. Reward-based selection history thus creates a reward priority signal but how does it functionally affect attentional selectivity?

To reiterate, when adhering to the theory of biased competition, selection can be understood as the process that resolves the intrinsic competition for neural representation (e.g. Duncan & Desimone, 1995). It is presumed that initial competition is dominated by the physical salience of a given stimulus, suppressing neuronal activity of other, less salient stimuli. Later in time, competition can be biased by top-down control; either by prioritizing spatial location (Moran & Desimone, 1985) or perceptual feature(s) summarized in an "attentional template" (e.g. Chelazzi, Duncan, Miller, & Desimone, 1998; Reynolds, Chelazzi, & Desimone, 1999).

Although reward biases the competition independently of bottom-up and top-down processes, much of the evidence to date suggests that it does so in a similar way as physical salience. This is corroborated by behavioral and neuronal evidence showing that reward interacts with physical salience of a stimulus (e.g. Wang et al., 2013), creates plastic changes in stimulus representations (e.g. Hickey et al., 2010; Hickey & Peelen, 2015) and affects selection as early as traditional manipulations of physical salience (e.g. Bucker et al., 2015; Failing et al., 2015). In light of the current evidence,

reward learning induces plastic changes in stimulus representations which are evident as early in visual hierarchy as the (extra-)striate visual cortex. By modulating neuronal firing in response to the reward-associated stimulus, these changes eventually come to bias competition very early on which might explain why reward effects escape top-down attentional control (cf. Theeuwes, 2010). Changes in the stimulus representation during learning result in stronger activity for that stimulus on the priority map (i.e. make selection more likely) which in turn reinforces the learning process and creates a bias that persists for a long period of time seemingly able to resist all but the most rigorous attempts of extinction.

As will be discussed in the next section, the dopaminergic system plays a critical role in reward learning and therefore in mediating the changes on a priority map. Since dopaminergic connections are widespread, projecting to brain regions that themselves project activity along the entire visual hierarchy, it is likely that dopaminergic activity during learning is reflected at multiple levels of the visual system. It is therefore conceivable that reward affects the representation of different attributes of a stimulus at different areas in the brain. That is, it may not surprising to observe the influence of reward on multiple sites in the brain associated with a priority map as they might reflect attentional priorities for different stimulus attributes, such as the stimulus' spatial position, its individual perceptual feature(s) or summary statistics. In line with this notion, reward-related activity has been observed in areas consistently associated with the attentional network and believed to represent a form of priority map (e.g. Corbetta & Shulman, 2002; Balan & Gottlieb, 2006; Bisley & Goldberg, 2010; Li, 2002; Mazer & Gallant, 2003), most notably area LIP/IPS, frontal eye field (FEF) and the superior colliculus (SC; e.g. Anderson et al., 2014; Dorris & Glimcher, 2004; Ikeda & Hikosaka, 2003; Kobayashi, Lauwereyns, Koizumi, Sakagami, & Hikosaka, 2002; Louie, Grattan, & Glimcher, 2011; Platt & Glimcher, 1999; Sugrue, Corrado, & Newsome, 2004; Weldon et al., 2008; Yasuda & Hikosaka, 2015).

In a recent study, Failing and colleagues (Failing et al., 2015, see Chapter 3; Pearson et al., 2016) speculated on how a stimulus-specific reward priority signal might affect oculomotor selection. They explained oculomotor selection due to reward in the context of the competitive integration model (Godijn & Theeuwes, 2002). According to this model, which is based on the theory of biased competition, overt search patterns are best described by a hierarchical priority map, or saccade map, presumably located in the SC.

Activity on the saccade map is assumed to spread to neighboring locations but inhibits activity of more distant locations through lateral inhibition. When the activity somewhere on the map passes a certain threshold, a saccade toward that location is executed. Modulations of activity are thought to occur through an integration of early bottom-up and late top-down signals that evolve after the onset of the search display (e.g. Mulckhuyse, van der Stigchel, Theeuwes, 2009; Trappenberg, Dorris, Munoz, & Klein, 2001). Accordingly, when a physically salient distractor activates a certain location on the map early in time, activity from stimuli in other locations is inhibited because of lateral inhibition. Only later, top-down processes inhibit the location of that distractor and activate (i.e. boost the activity of) the target location. Since Failing and colleagues observed oculomotor capture by reward-signaling but otherwise non-salient stimuli particularly for the early first saccades, it is likely that the reward signal is already integrated at an early stage of the selection process. At this stage, the location of the reward-signaling stimulus has a high activity on the saccade map that inhibits activity of other distant locations (e.g. the location of the target) through lateral inhibition. It is thus at this early stage that saccades toward the reward-signaling stimulus are particularly promoted.

Challenging the interpretation of oculomotor selection due to reward in the framework of the competitive integration theory is the finding that reward signaled by a distractor does not seem to differently affect saccadic latencies to the target in oculomotor tasks (e.g. Failing et al., 2015; Pearson et al., 2016; Theeuwes & Belopolsky, 2012). However, this would have been expected due to stronger inhibition of saccadic activity for the distant target location. Belopolsky (2015) speculated that the association with reward may give an independent boost to the saccade program to the distractor's location without affecting the lateral inhibition of the other stimuli (i.e. the target). Alternatively, Failing and colleagues (Failing et al., 2015; Pearson et al., 2016) suggested that reward might lower the threshold which must be surpassed in order to elicit a saccade in a feature-specific manner. Although it seems clear that reward signals are competitively integrated on a common priority map illustrating their influence on eye movements, further research is necessary to establish whether the competitive integration model can fully account for reward-specific modulations in overt search.

In sum, empirical evidence supports the notion that reward affects the neuronal representation of the reward-associated stimulus (feature) rendering it more salient to the visual system. As a consequence, perceptual and

attentional processing of stimuli imbued with a reward association is facilitated in a way that is akin to facilitatory priming of stimulus representations. Critically, this reward-induced priming establishes a priority signal which biases competition and thus affects attentional selection in covert as well as overt search independently of concurrently active top-down or bottom-up processes. This bears out the need for revising the classic theories dichotomizing attentional control in either top-down or bottom-up control (Awh et al., 2012).

1.2.3. On the role of dopamine in learned reward priority

There is strong evidence for a change in the representation of a stimulus associated with reward which, among other things, determines its perceptual and attentional processing. However, an important question is how this change is accomplished during the reward learning process. Major theories ascribe the dopaminergic systems in the midbrain, particularly the substantia nigra and ventral tegmental area, and their projections onto other brain areas such as the basal ganglia and the frontal part of the cerebral cortex, a pivotal role during reward learning. Although most theories support the idea that dopamine contributes to neuronal plasticity alongside other neuromodulators, its specific role in reward learning is still a matter of debate (e.g. Aarts, van Holstein, & Cools, 2011; Berridge & Robinson, 1998; Hikosaka, Kim, Yasuda, & Yamamoto, 2014; Roelfsema, van Ooyen, & Watanabe, 2010; Schultz, 1997). For instance, dopamine has been suggested to either mediate general functions of action generation, effort, movement, and general arousal (cf. activation-sensorimotor hypothesis), represent the hedonic value of reward (cf. hedonia hypothesis), code a learning or teaching signal that forges associations or represents a simple reward-prediction error (cf. reward learning hypothesis), or mediate the dynamic "wanting" attribute of incentive salience (cf. incentive salience hypothesis; for a detailed discussion on the putative functions of dopamine see Berridge, 2007).

Irrespective of which theory one adheres to, there is substantial evidence for the involvement of the dopaminergic system in the context of reward-driven modulations in attentional control. For example, similar to other studies investigating the influence of incentive reward on attentional control (e.g. Krebs, Boehler, Egner, & Woldorff, 2011; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Small et al., 2005), a series of studies by

Pessoa and colleagues demonstrated that incentive rewards evoked activity in large distributed brain networks, particularly those associated with attention and dopamine-release (Engelmann et al., 2009; Engelmann & Pessoa, 2007; Pessoa & Engelmann, 2010; Padmala & Pessoa, 2011). Importantly, by employing network analysis, they showed that while those networks were largely segregated during control trials (i.e. they exhibited high within-network connectivity), there was less segregation (i.e. higher between-network connectivity) during reward trials (Harsay et al., 2011; Kinnison, Padmala, Choi, & Pessoa, 2010). In other words, given the direction of midbrain projections, dopaminergic activity due to incentive rewards might increase the coupling and integration between the networks allowing for optimal performance. Pessoa (2015) speculated that dopamine improves the signal-to-noise ratio of relevant neurons (e.g. Sawaguchi & Matsumura, 1985) which "sharpens" attentional control and, in turn, may enhance processing efficiency in target cortical and subcortical regions. Corroborating evidence comes from Noudoost and Moore (2011) who pharmacologically altered the dopamine receptor activity in the FEF of the prefrontal cortex and measured its effect on extrastriate area V4. D1 receptors in FEF mediated prefrontal control by leading to enhanced and more selective neuronal responses in V4 in a manner that was comparable with known top-down attentional modulations.

As discussed previously, the influence of reward is not only restricted to modulations in strategic attentional control. Nevertheless, studies investigating the influence of stimulus-specific reward-associations on selection also indicate a vital role of dopamine even if the reward effects occur independently of competing top-down processes. The findings in those studies support the idea that dopamine might be responsible for changes in the representation of a reward-associated stimulus. For instance, the behavioral impact of intertrial reward priming in Hickey and colleagues was positively correlated with a midline anterior ERP component, called medial frontal negativity, which is suggested to reflect the assessment of motivational impact (Gehring & Willoughby, 2002; Hickey et al., 2010). More convincingly, Hickey and Peelen (2015) showed that midbrain sensitivity to reward-associated distractors objects predicted the strength of suppression of the distractor representation in OSC. Interestingly, they also observed modulations in other prefrontal regions, such as the orbitofrontal cortex and dorsolateral prefrontal cortex that receive direct dopaminergic input from the midbrain. This suggests that the propagation of the dopaminergic signal from

the midbrain to other areas which are not part of the visual system might also be critical for the influence of reward on selection to occur. This notion was further supported by recent lesion studies. For example, Vaidya and Fellows (2015) found that while healthy controls and patients with a lesion in the lateral or the dorsomedial frontal lobe showed intertrial reward priming, patients with a lesion in the ventromedial frontal cortex (vmPFC) did not (but see Manohar & Husain, 2016). Such findings demonstrate that the specific role of the brain areas onto which the dopaminergic midbrain projects directly is complex and depends on a variety of factors, at least in the context of their contribution to attentional selection.

A limitation of the majority of the neuroimaging studies on dopamine concerned with attentional control is that it is difficult to assess whether midbrain activity reflects anything else than the processing of immediate reward feedback. Indeed, in these studies, participants are typically continuously rewarded for behavior. In this regard, studies measuring reward effects in the absence of active reward learning, such as those consisting of a separate training and test session, are of particular importance. Regardless of this crucial difference, these studies also underscore the importance of the dopaminergic system. In one fMRI study, neuronal activity in the striatum was observed to be elevated in response to distractors that were previously associated with high reward, relative to those previously associated with low reward (Anderson et al., 2014). Even stronger evidence comes from a recent positron emission tomography study (Anderson et al., 2016). In this study, attentional capture by previously reward-associated but physically non-salient and task-irrelevant distractors was positively correlated with the release of dopamine within the caudate and posterior putamen. Likewise, the ability to resist attentional capture by such distractors was associated with a corresponding suppression of dopamine release. It is critical to understand that participants in these studies could no longer earn any reward but the previously rewarded stimuli still elicited a response in the dopaminergic midbrain. While these findings blend well with all types of reward studies, they still support multiple interpretations concerning the exact role of dopamine.

In summary, neuromodulatory activity through the dopaminergic midbrain due to differential reward not only broadly affects performance through its diffuse connections with brain areas critically involved in cognitive and attentional control. Evidence suggests that it mediates

attentional selectivity by contributing to changes in the representation of reward-associated stimuli. However, the exact role of dopamine and which processes are necessary or sufficient to translate the dopaminergic signal into reward selection priority are only poorly understood.

1.2.4. Nonspatial attentional selection and reward

So far, the majority of the reviewed studies investigated the influence of reward on spatial attention selection. However, attention is not only limited by spatial but also by temporal constraints. Consider again the example of how you find your way through the city to visit your friend. At some point during the trip you may have to stop at an intersection and wait for the traffic light to turn green. While waiting, there is little uncertainty as to *where* in space the target (i.e. the green light) appears, but there is great uncertainty as to *when* it appears. This scenario illustrates nonspatial[1] attentional selection (e.g. Folk, Leber, & Egeth, 2008; Shapiro, Raymond & Arnell, 1997).

One way to study nonspatial attentional selection is in the context of the attentional blink phenomenon (AB; Raymond & Shapiro, 1992). In an AB task, participants are usually presented with a stream of stimuli in which each stimulus is presented for only a short duration at the center of fixation. Participants have to detect or discriminate between the identity or features of two targets embedded in the stream. The typical finding is that performance on the second target is severely deteriorated when it is presented shortly (around 200 ms) after the first target compared to when the interval between the presentation of both targets is longer (e.g. 800 ms; Shapiro, Raymond, & Arnell, 1997; Dux & Marois, 2009). Since uncertainty as to where the targets occur is absent, while uncertainty as to when they appear is large, these tasks clearly demonstrate the limits of available attention across time. The AB phenomenon illustrates that through temporal selectivity some stimuli will reach later stages of processing and eventually conscious awareness while others will not (for recent reviews see Bowman & Wyble, 2007; Martens & Wyble, 2010; Taatgen, Juvina, Schipper, Borst, & Martens, 2009).

[1]It should be noted that others refer to nonspatial attentional selection when the target is defined by its identity or other perceptual features (e.g. color) and not its spatial position. But even in these cases, we believe that attentional selection is spatial since it must first be shifted in space (Duncan, Humphreys & Ward, 1997).

Raymond and O'Brien (2009) were the first to demonstrate that reward affects nonspatial attentional selection using the AB paradigm. Similar to the studies on VDAC, they divided their experiment in a training and test session. During the training session, participants learned associations between different face stimuli and reward magnitudes (losses, neutrals and wins) in the context of a choice game. In the subsequent test session in which there was no longer any reward, participants saw two targets: a patch of circles or squares (T1) and either a face they had seen during the training or an entirely new face (T2). Both targets were temporally separated by either a short (200 ms) or a long (800 ms) interval. When participants were shown a face from the training session, successful recognition depended on the expected value coupled to it during training with an expected reward or loss improving recognition and no expected value leading to poor recognition. Critically, when both targets were separated by a short interval, only the face pictures previously coupled to reward remained unaffected by the interval between target presentations. When the order of targets was swapped in the test session of a follow-up study, performance on T1 (reward-associated faces) was still differently modulated by reward, but performance on T2 (a patch of circles or squares) was not. Consequently, Raymond and O'Brien concluded that recognition is better for stimuli previously coupled to a high probability outcome of earning or losing but only reward-associated stimuli are able to overcome the AB (see also Yokoyama, Padmala, & Pessoa, 2015).

The finding of Raymond and O'Brien (2009) that recognizing T2 was unaffected by the reward associated with T1 is somewhat surprising given the substantial evidence for a prioritized attentional status of reward-associated stimuli at the expense of others (including more salient targets). The reward-dependent prioritized status of a stimulus should come at a larger cost for subsequent processing of other task-relevant stimuli, particularly because the AB is thought to reflect failed attentional suppression during T1 processing (e.g. Martens & Wyble, 2010; Taatgen, Juvina, Schipper, Borst, Martens, 2009; Wyble, Bowman, & Nieuwenstein, 2009). In other words, one would have expected that performance on T2 deteriorates as a function of the reward association of T1 assuming that, similar to spatial attention, reward also affects the availability of attention across time. Therefore, observing no interference on T2 performance may either be because reward affects nonspatial selection in a different way than spatial selection (i.e. reward only causes spatial but not nonspatial attentional capture) or the task design was not sensitive for answering this question. Indeed, in the study of Raymond and

O'Brien participants had to attend the reward-associated stimuli during training and test session as they were always task-relevant. Therefore, while perceptual processing may have benefitted from reward-based selection history such that stimuli associated with high reward were more robustly represented and hence more readily identified, attentional processing may have already been at highest priority because attending the stimulus was task-relevant. Possibly due to a ceiling effect, no bias due to reward-based selection history could affect attentional processing any further and thus cause differential effects on the AB (i.e. T2 identification). This is in line with the already very high discrimination sensitivity found for T1 which implies almost perfect selection (Raymond & O'Brien, 2009).

To address this issue, Failing and Theeuwes (2015; see also Chapter 5) conducted a series of experiments in which the reward-associated stimulus was always a task-irrelevant distractor during the test session. In this study, participants had to detect the presence of a single target (i.e. a picture of a designated category of scenes, e.g. forest scenery) embedded in a stream of different stimuli (i.e. pictures of another category of scenes, e.g. field scenery). In two thirds of the trials, a previously rewarded stimulus (i.e. picture of a third or fourth category of scenes, e.g. water and mountain scenery) was embedded as distractor in the stream. The results showed interference in the sensitivity for detecting the target when a previously reward-associated stimulus was present even though these stimuli were completely task-irrelevant and no longer signaled any reward. Importantly, the degree of interference depended on the magnitude of reward previously associated with the distractor – with high reward causing the strongest interference. Particularly remarkable was that this effect was found even though reward was associated with complex visual scenes of a given semantic category rather than simple features. Moreover, the effect was not exclusive to the specific stimuli whose selection was rewarded but generalized to unseen stimuli from the same semantic category (see Experiment 2, Failing & Theeuwes, 2015). Given the severely limited presentation duration of each stimulus, this suggests that reward either affects highly complex sets of features or may act on the level of gist perception.

It is parsimonious to assume that the functional mechanism explaining the influence of reward-based selection history on nonspatial attentional selection is similar to how reward-based selection history affects spatial attentional selection. It is thus feasible that the representation of the stimulus

associated with reward changed throughout the training session such that stimuli associated with relatively larger reward became more salient. Stimuli imbued with reward salience are thus not only more readily perceived but also receive priority in attentional processing when processing is temporally constrained. Attentional priority, in turn, delays successful attentional suppression which then causes interference in the detection of subsequent stimuli. Stimuli associated with high relative to low reward have also been shown to receive additional post-perceptual and –selection processing, for instance reflecting mandatory maintenance in visual short term memory (e.g. Kiss et al., 2009; Thomas, FitzGibbon, & Raymond, 2016). Processes like these may further contribute to the deterioration in subsequent stimulus detection.

In summary, AB studies provide evidence for an important role of reward in shaping nonspatial attentional selection. Stimuli associated with reward gain priority in perceptual and attentional processing when processing is temporally constrained. On the one hand, this empowers them to overcome the AB (Raymond & O'Brien, 2009). On the other hand, if processing them is not a high priority, they can be a powerful distractor deteriorating subsequent temporal processing (Failing & Theeuwes, 2015; Chapter 5). The priority is likely to be the result of a changed stimulus representation such that the stimulus becomes more salient to the visual system which delays its successful suppression.

1.3. Time perception and reward

Given the substantial influence of reward on attention and the long-standing acknowledgement of the influence of attention on perception, an intriguing question regards a possible influence of reward-driven attention on perception. Time perception, in particular, has been argued to be influenced by attention and memory, both important processes in reward-driven attention (Brown, 2010; Coull, Vidal, Nazarin, & Macar, 2004; Tse, 2010).

A convincing example of the influence of attention on time perception was provided by Tse and colleagues (Tse, Intriligator, Rivest, & Cavanagh, 2004) who investigated how infrequently presented stimuli affect duration comparisons. In their experiments, a standard stimulus (e.g. a black disk) was repeatedly presented for a fixed duration (e.g. 500 ms) at the center of fixation.

This stream of standard stimuli was occasionally interrupted by a novel stimulus, called temporal oddball, which differed in a single perceptual feature (e.g. a red disk) and was presented for varying durations (e.g. 350-650 ms). Participants' task was to judge whether the temporal oddball was presented shorter or longer than the standards. Tse et al found that participants were biased toward reporting that the oddballs appeared to last longer than the standards. This oddball effect was robust across features (color, size or motion), modalities (visual and auditory) and psychophysical measurement techniques (method of constant stimuli, magnitude estimation and duration reproduction). Tse et al argued that the temporal oddball drew more attention because it was the salient and unexpected item in the sequence. The increase in attentional prioritization of the oddball distorted its perceived duration, such that the oddball was perceived to last longer than it actually did (for similar conclusions see e.g. Kanai & Watanabe, 2006; Mattes & Ulrich, 1998). In support for this conclusion, temporal oddball effects were not observed once stimulus presentation time was reduced below 120 ms which is consistent with the amount of time it takes for attention to be allocated to a stimulus after onset (e.g. Nakayama & Mackeben, 1989).

Failing and Theeuwes (Failing & Theeuwes, 2016; see Chapter 6) investigated the influence of reward-driven attentional modulation using the temporal oddball paradigm. In a series of experiments, they showed that stimuli associated with relatively larger reward are judged to last longer than they actually did, that this effect parametrically scales with the magnitude of reward and that it is specific to the stimulus associated with reward rather than being the result of a change in the observers' state (e.g. reward inducing a heightened level of alertness or vigilance). These findings underscore the highly intertwined relationship of attention and time perception (Meck & Benson, 2002) and indicate that this relationship is mediated by reward. In particular, they suggest that, through reward-induced changes in the stimulus representation (i.e. reward-associated stimuli gain reward salience), reward parametrically modulates perceived duration.

The experiments furthermore provided evidence that the influence of reward on time perception is, at least for durations below a second, discrete rather than proportional to the objective duration. This notion is critical for distinguishing between two putative mechanisms of how reward-based attention may affect subjectively perceived time. According to classic information processing theories, perceived duration is a function of the

amount of information processed per unit objective time (e.g. Gibbon, Malapani, Dale, & Gallistel, 1997; Thomas & Weaver, 1975) and it was suggested that attention increases the amount of temporal information processed (Tse et al., 2004; Tse, 2010). Accordingly, in conditions with larger reward salience (e.g. on high reward trials), accumulated temporal information should increase proportionally to the increase in objective duration of the reward-associated stimulus. However, Failing and Theeuwes (2016) found no evidence for such a proportional increase. Instead, they found that the size of the effect did not statistically differ between different object durations. The authors therefore speculated that reward associated with a to-be-timed stimulus affects the initiation of the timing signal, or "starting gun" response. According to the striatal-beat-frequency model (e.g. Buhusi & Meck, 2005; Matell & Meck, 2000; van Rijn, Gu, & Meck, 2014), time intervals are assessed by comparing differential activity of various periodic neuronal activity, in particular the coincidental activation of striatal spiny neurons in the basal ganglia. In order to properly assess timing, these striatal cells need to be able to reset upon the onset of a timing signal (Matell & Meck, 2000). Bursts of dopaminergic activity in the midbrain (i.e. substantia nigra pars compacta) serve as preparatory signal, or starting gun, to reset irrelevant or random neuronal activity. In this framework, a quicker starting gun response would then lead to a faster initialization of the clock-system, after which time is perceived without any additional (attention-based) modification (cf. Taatgen, van Rijn, & Anderson, 2007). This interpretation dovetails nicely with recent findings highlighting the importance of the dopaminergic midbrain in shaping the neuronal representation of a stimulus associated with reward (Anderson et al., 2014; Anderson et al., 2016; Hickey & Peelen, 2015). Stronger activity of the dopaminergic midbrain might therefore not only affect the representation of a reward-associated stimulus but also distort the temporal perception of such a stimulus.

1.4. Attention and threat

Survival in the animal world did not solely depend on efficiency in obtaining reward. Immediate detection of potential danger or threat is still important for survival today and has unabated adaptive value by incorporating putatively innate as well as learned adjustment processes that shape present as well as future behavior (LeDoux, 1996). Numerous studies have demonstrated that

this is also reflected in attentional control and suggested that neuronal activity associated with threat-related stimuli is obligatory (Vuilleumier, Armony, Driver, & Dolan, 2001; Whalen et al., 1998; but see Pessoa et al., 2002).

Much like research on the influence of reward on attention, early work on the influence of threat on attention was focused on how threat affected strategic cognitive control. Many of these studies traditionally used pictorial stimuli such as angry faces or spiders to convey threat and indeed many found that attentional processing is biased toward processing of such stimuli (for a review see, e.g. Vuilleumier, 2005). For instance, search times for threat-related targets presented among neutral distractors is shorter compared to a neutral target (e.g. Esteves, 1999; Öhman, Flykt, & Esteves, 2001; Öhman, Lundqvist, Esteves, 2001; Soares, Esteves, & Flykt, 2009; Soares, Esteves, Lundqvist, & Öhman, 2009). Importantly however, when threat-related pictures were presented as distractors while searching for neutral targets, it was shown that search time was increased (e.g. Lipp & Waters, 2007; Miltner, Krieschel, Hecht, Trippe, & Weiss, 2004; Rinck, Reinecke, Ellwart, Heuer, & Becker, 2005). Such reports fueled influential theories denoting a special status of fear-inducing information in attentional and perceptual processing. For example, Mathews and Mackintosh (1998) proposed the existence of a Threat Evaluation System that automatically encodes the level of threat already very early in the processing stream. Similarly, according to the fear module theory of Öhman and Mineka (2001), our brain is equipped with a fear module to quickly detect threatening stimuli and subsequently evoke neurophysiological as well as behavioral changes ensuring optimal adaptation. Conjointly, these theories propose that the visual system evolved to be biased for quick and automatic processing of threat because it provided an adaptive advantage.

Although compelling from an evolutionary point of view, much of the evidence in favor of this theory raised concerns regarding the validity of the conclusions drawn. For instance, many studies involved threatening stimuli that were often relevant to the task at hand (e.g. by being the target), thereby questioning the notion of automaticity of the attentional bias. In a similar vein, studies have provided mixed results regarding the nature of the attentional bias. Some provided evidence for facilitated attention (e.g. Yiend & Mathew, 2001), while others only observed delayed attentional disengagement (e.g. Belopolsky, Devue, & Theeuwes, 2011; Cooper & Langton, 2006; Stormark, Nordby, & Hugdahl, 1995), suggesting an effect of threat on post-perceptual

and -selectional stages. Finally, the use of pictorial stimuli made it difficult to preclude alternative explanations in terms of physical properties (i.e. saliency; for an elaborated discussion on these issues see Schmidt, 2015).

The recent years have seen attempts to more rigorously tackle these issues by abandoning the use of pictorial stimuli and using aversive conditioning procedures instead. For instance, Koster and colleagues (Koster, Crombez, van Damme, Verschuere, & De Houwer, 2004) showed that an otherwise inconspicuous cue signaling the possibility of an aversive tone resulted in faster responses times on valid and slower response times on invalid trials relative to neutral baseline using the same stimuli but without any association with an aversive tone. The approach of yet other studies was to measure the impact of a stimulus associated with threat on performance after conditioning it with threat (i.e. when it no longer signaled threat). In this regard, these type of studies used a similar approach as the experiments studying the influence of reward-based selection history on attention using a separate training and test session. Following this approach, Notebaert and colleagues reported that search time for targets presented near a stimulus that previously signaled the possibility of an electric shock was reduced (Notebaert, Crombez, van Damme, De Houwer, & Theeuwes, 2011). Another study demonstrated that physically salient distractors caused more interference in search time when they were previously associated with an electric shock (Schmidt, Belopolsky, & Theeuwes, 2015a). These studies are consistent with the idea of attentional capture by a threat-associated stimulus. However, in these studies attending the threat-related stimulus was either not consistently tied to any costs, encouraged throughout a separate session (i.e. conditioning session; Notebaert et al., 2011) or mediated through physical salience (Schmidt et al., 2015a).

In an attempt to overcome these limitations, Schmidt and colleagues (Schmidt, Belopolsky, & Theeuwes, 2015b) investigated the effect of threat on eye movements. Their study consisted of a single experimental phase in which the threat-signal of an otherwise neutral (i.e. not physically more salient) cue was orthogonal to other task relevant factors. In other words, a cue, which signaled the possibility of receiving an electric shock and preceded the onset of the target, could coincide with but was not predictive of the location of the target stimulus (cf. Peck et al., 2009). The results showed that even though there was no strategic advantage to move the eyes to the threat-signaling stimulus, saccades toward the target location were faster when it

appeared at the spatial location previously occupied by the threat-signaling cue compared to when it was occupied by a neutral cue. Since the threat-signaling cue was not physically any more salient than the neutral cue, this provides strong evidence that threat associated with an otherwise neutral stimulus causes attentional capture. Corroborating evidence comes from an earlier study employing an aversive conditioning procedure. In this study, participants had to saccade to a stimulus above or below fixation while ignoring a distractor that either had a color conditioned to an aversive noise or a color that was not aversely conditioned (Mulckhuyse, Crombez, & van der Stigchel, 2013). Here too, results showed that the distractor attracted the eyes more often when it was of the color associated with threat.

Even though all these previous studies demonstrated a bias in covert and overt search toward threat-signaling stimuli, it should be realized that the reported effects can likewise be explained in terms of top-down processes, bottom-up processes or differences in selection history (Awh et al., 2012) rather than mandatory attentional prioritization due to the threat signal. Indeed, in all experiments investigating threat, participants were instructed or encouraged to attend the threat-related stimulus either because it was part of the task (e.g. Koster et al., 2004) or because it was part of the pre-experimental conditioning session (e.g. Mulckhuyse et al., 2013; Notebaert et al., 2011). Similarly, the threat-signaling stimulus may have been attended because its saliency was not carefully controlled (e.g. Öhman, Lundqvist, Esteves, 2001; Schmidt et al., 2015a) or because it was not associated with any costs for task performance or any influence on the aversive experience (e.g. Schmidt et al., 2015b).

On these grounds, a recent study (Nissens, Failing & Theeuwes, in press; see Chapter 7) tested the notion of automatic capture by threat-signaling stimuli in the most rigorous fashion. The experimental paradigm of their study was analogous to how they investigated the influence of reward on oculomotor behavior while controlling for other top-down and bottom-up processes (cf. Failing et al., 2015). In other words, participants had to saccade to a shape singleton (e.g. a diamond among circles) and fixate it. While the presence of one particularly colored non-target (e.g. blue) shape signaled the possibility of receiving a shock, the presence of another particularly colored non-target (e.g. a red) shape signaled that no shock would be delivered. This task-irrelevant and shock-signaling stimulus was embedded in a heterogeneous display rendering it physically not more salient than any other stimuli in the

display. Therefore, based on its visual features, the shock-signaling stimulus did not stand out from the other stimuli but was in fact less salient compared to the shape singleton target. Critically, this study not only discouraged attending the threat-signaling stimulus by never rendering it the target or physically salient, it even incentivized not attending the stimulus: if participants would make a saccade to the threatening stimulus, there was a higher probability of receiving an electric shock. Participants were explicitly told that if their response was quick enough, they could avoid receiving a shock. Therefore, if anything, to avoid receiving (more) shocks, the best available strategy was to never attend the threat-signaling stimulus.

Even under these aggravated conditions, oculomotor capture by the threat-signaling stimulus was observed (Nissens et al., in press; see Chapter 7). Critically, the influence of the threat-signaling stimulus was observed early in the selection process such that predominantly the early first saccades were prone to oculomotor capture even though the capture was equivalent to a higher likelihood of receiving a shock. In line with major theories on emotion processing (Mathews & Mackintosh, 1998; Öhman & Mineka, 2001), this study therefore provides convincing evidence for a mandatory and involuntary effect of threat on the allocation of attention which cannot be fully controlled in a top-down effortful fashion.

Interestingly, all threat effects on oculomotor control were virtually identical to the reward effects Failing and colleagues found when investigating the influence of reward (Failing et al., 2015). This similarity suggest that both, reward and threat, may influence attentional selection via a, at least partially, overlapping mechanism. This notion has already been put forward in other recent reports (e.g. Belopolsky, 2015; Schmidt, 2015; Schmidt et al., 2015b) and support for the idea that threat affects the stimulus representation directly, much like reward, is mounting (e.g. Lim, Padamala, & Pessoa, 2008; Pessoa & Padmala, 2007; Phelps, Ling, & Carrasco, 2006).

1.5. Summary

Decades of research have indicated that attentional control is the result of a mixture of top-down and bottom-up processes. Up till now it was generally accepted that rewards affect top-down processing in that it motivates people to perform better and more accurately by promoting stronger cognitive and executive control. Only recently, however, research has demonstrated that

reward can shape perceptual as well as attentional processes that are basically independent of known top-down and bottom-up processes. Reward prioritizes stimuli for covert or overt search, modulates spatial as well as nonspatial attentional selection and distorts the subjective perception of time. The existing literature strongly suggests that this is achieved by changing the neuronal representation of a stimulus such that it becomes more pertinent to the visual system. By demonstrating a similar influence of threat on attention, other research suggests that reward may not be a solitary exception. Conjointly, these findings urge for revising traditional models on attention which dichotomized attentional control in either top-down and bottom-up processes. Instead, they support the idea that selection history, shaped by reward or threat, affects current and future attentional selection.